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INSECT HORMONES AND BIOANALOGUES: THEIR EFFECT ON RESPIRATORY METABOLISM IN *DERMESTES VULPINUS* L. (COLEOPTERA)

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Postembryonic development of insects proceeds as distinctive cycles characterized by specific changes in structure and function. From particular physiological changes and hormonal conditions we can distinguish several categories of developmental cycles: (i) larval-larval molt cycles, (ii) larval-pupal and larval-adult molt cycles, (iii) pupal-adult molt cycles in the Endopterygota, (iv) reproduction cycles in adult females and, (v) a combination of molt and reproduction cycles in the Apterygota. It has been recognized earlier (Sláma, 1968) that in addition to growth and developmental patterns, each of the above categories can also be characterized by certain specific type of total body metabolism. By altering hormonal conditions it has been possible to induce prematurely or to postpone the appearance of the given developmental cycles. And, without respect to age or absolute size of the body, the specific patterns in total body metabolism have also been correspondingly transposed (hand-in-hand with the transposition of the cycle in question). This has been documented in studies of juvenile hormone-induced transposition of the larval and adult molt cycles in Exopterygota (Sláma, 1964, 1965, 1968, 1971; Sláma, Romaňuk and Šorm, 1974) and by observations on the larval, pupal, and adult molt cycles in Endopterygota (Sehnal and Sláma, 1966).

In the present paper we have extended these studies on the relationships between hormones, growth, morphogenesis, and respiratory metabolism to larvae and pupae of a coleopteran of the family Dermestidae. The advantages of this material for metabolic investigations are shown by the fact that it was possible to delay the pupal-adult molt cycle by one or more extra pupal cycles simply by treatment with the juvenile hormone bioanalogues (juvenoids). Moreover, it was possible to induce extra larval and larval-pupal molt cycles by injections of bioanalogues of the prothoracic gland hormone (ecdysoids).

Materials and Methods

The larvae and adults of *D. vulpinus* were reared in glass jars at 27° C and 18 hr photophase. They were fed dried calf viscera and supplied with water in cotton plugged glass vials. All the non-feeding stages were incubated at 27° C in Petri dishes which were provided with a source of moisture.

Oxygen consumption was measured with a Warburg apparatus using conventional techniques (Sláma, 1960). The respiratory vessels were cylindrical and without side arms. Their internal volume was approximately 10 ml. The values of O_2 consumption presented in the figures are averages of 3 to 5 successive read-

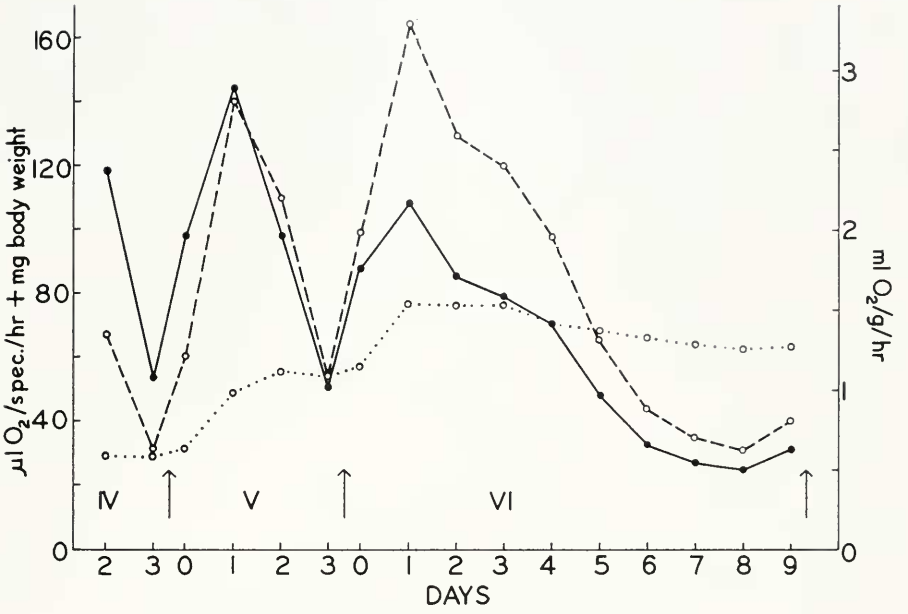

FIGURE 1. Changes in average body weight (dotted line), O_2 consumption in μl/hr/specimen (broken line), and O_2 consumption in ml/gram live weight/hr (full line) during the 4th, 5th, and last (6th) larval instars of *D. vulpinus*. The arrows indicate ecdyses (n = 12 specimens).

ings on each of the individually measured specimens, the number of which (n) is indicated in the legend. Due to considerable changes in body weight we have indicated O_2 consumption values both per specimen and per gram of fresh body weight in all the feeding stages. However, in the non-feeding stages where the body weight undergoes only slight and more or less constant diminution we have related the O_2 consumption values per gram of the initial weight only. The standard deviation from the mean values of Q_{O_2} in the feeding stages (Figs. 1 and 2) was around ± 30 per cent. In the non-feeding and immobile specimens (Figs. 3 to 7) the individual O_2 consumption curves of each specimen had parallel courses. There were extremely small deviations from the mean values (usually not exceeding ± 20 per cent). The deviations were more or less constant in each specimen suggesting that they were merely due to different size of the body and due to different content of reserve materials which take no active part in metabolism.

Out of a large number of juvenile hormone analogues we selected for the experiments with *Dermestes* an ethyl ester of 3, 7, 11-trimethyl, 11-chloro, 2-dodecenic acid. This juvenoid was highly active in topical applications and it appeared to be relatively stable in the body. The ID-50 Morph. unit of juvenile activity of this compound in the pupal assay on *D. vulpinus* is approximately 5/μg per specimen (Sláma *et al.*, 1974). In all cases topical application in 1/μl of acetone was used. Ecdysterone (Polypodine A isolated from *Polypodium* by Dr. J. Jizba of the Czechoslovak Academy of Sciences) was injected into the body cavity in 1/μl of 10 per cent ethanolic Ringer solution.

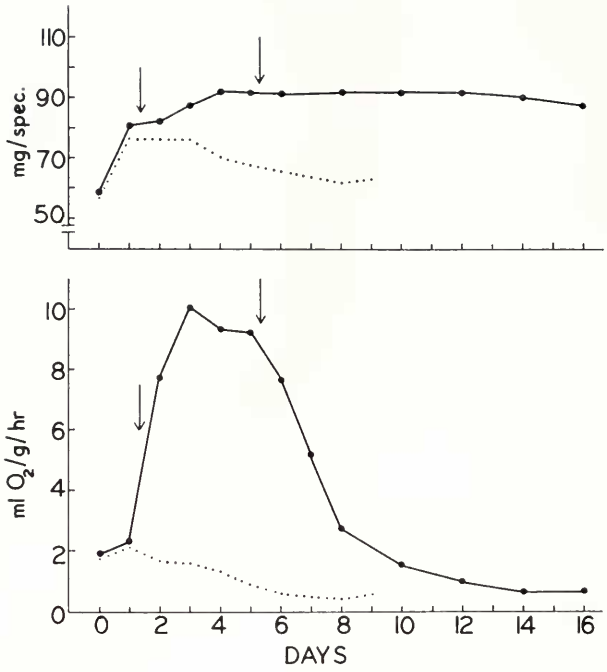

FIGURE 2. Changes in the body weight (above) and O_2 consumption (below) of last instar larvae treated with 50/μg/specimen of the juvenoid at the moments indicated by arrows (full line; n = 9 specimens). The dotted line shows comparison with untreated larvae.

RESULTS

Growth and respiratory metabolism in normal larvae

It is well known that changes associated with growth have a profound influence on larval metabolism. We have, therefore, recorded the changes in larval body weight which are more or less correlated with the rate of feeding and excretion. The results in Figure 1 show that the largest daily increments in body weight occur during the first day after each larval ecdysis. This is connected with intensive feeding activity at this time. A maximum body weight of the whole post-embryonic development is reached approximately at day 3 of the last (6th) larval instar. After that the weight successively diminishes throughout the rest of the last larval instar as well as during the whole metamorphosis period. Feeding is completely abolished from day 5 of the last larval instar.

In the penultimate (5th) larval instar the rate of O_2 consumption undergoes specific alterations which seem to be common for the larval-larval molt cycles. They have been found in the young larval instars of many unrelated insects by a number of authors (*cf.* Sláma, 1960; Sehnal and Sláma, 1966). It can be observed in Figure 1 that a common pattern of these metabolic changes is a relatively steep rise in O_2 consumption rate during the initial intensive feeding period, a peak in Q_{O_2} at about the middle of the inter-ecdysial period and, a subsequent fall of the

metabolic activity towards the next ecdysis. This type of metabolic change can be briefly characterized as a reciprocal U-shaped course.

In the final, *i.e.* 6th larval instar, the course of O_2 consumption (Fig. 1) is somewhat different. Though the initial rise of O_2 consumption during the first day after ecdysis is present, the intensity of respiratory metabolism progressively diminishes, following a U-shaped pattern towards pupation. This type of metabolic cycle also seems to be widespread among last larval instars of many Endopterygote and Exopterygote insects, as discussed below.

Hypermetabolism induced by juvenoids in the last larval instar

In many Endopterygote insects it is extremely difficult or impossible to induce extra larval molts by application of juvenoids to the last instar larvae. This problem has been analyzed elsewhere (Sláma *et al.*, 1974). So also in *D. vulpinus* it has been so far impossible to cause the extra-larval instars or even larval-pupal intermediates by any available kind and amount of juvenoids. Out of all the morphological effects often connected with this treatment we observed only an occasional formation of pupae possessing larval cuticle on the distal ends of the legs, palpi, and antennae. The treated last instar larvae have always pupated after a considerable delay. The delay was proportional within certain limits to the dose of juvenoid and to number of applications, and it was well correlated with the specific juvenile hormone activity of various juvenoids as revealed by morphological assays on pupae of the same species (ID-50 Morph. units).

In addition, the above mentioned delay of pupation by juvenoids was always associated with enormously increased rate of feeding and excretion. The feeding period was prolonged from 5 to 10 or more days and the amount of excrement produced in daily intervals was drastically enhanced. Finally, when the affected larvae ultimately pupated, the pupae were significantly heavier than the normal ones (approximately 80 mg/specimen in contrast to about 65 mg of normal pupae). More importantly, they developed almost invariably into extra pupal instars or into adultoids.

One of the most spectacular physiological effects of juvenoids at the onset of the last larval instar of this species is an enormous increase in rate of O_2 consumption (see Fig. 2B). Indeed, treated larvae have consumed as much as 10 ml O_2 per gram live weight per hr and have maintained this extraordinarily elevated rate for several days. The degree of stimulation is unusual even among insects which often have high respiratory rates in comparison with other animals. Additional experiments, including tests of other vessel sizes and KOH concentrations, confirmed unequivocally that we were not dealing with any kind of artifact. We have thus discovered an unusual and specific effect of juvenoids for which we suggest the term "hypermetabolism".

Further studies revealed that the duration of hypermetabolism is limited. Even when juvenoids were continuously administered in excessive amounts, pupation was not delayed beyond certain time limits. The decline of O_2 consumption rate after several days of hypermetabolism could not be prevented by renewed juvenoid treatments, as is evident from Figure 2B. Moreover, hypermetabolism can be induced only when juvenoids are applied during the feeding period, *i.e.*, from ecdysis

to the 5th or 6th day thereafter. Later treatments of the non-feeding last instar larvae had no effect on O_2 consumption of the prepupal stages.

The respiratory quotients determined by the indirect Warburg method revealed somewhat lower ratios in hypermetabolic larvae (0.719) in comparison with the equally old untreated larvae (0.755). This suggests that simultaneously with the almost 10-fold increase of O_2 consumption during hypermetabolism, the output of CO_2 was also enormously increased.

Dependence of hypermetabolism on nutrition

Preliminary experiments revealed that hypermetabolism was seriously limited or absent when the treated larvae were deprived of food. We have now performed another series of experiments using non-feeding and immobile larvae which had been ligated behind the head capsule. According to Sláma *et al.* (1974) the larvae of *D. vuplinus* can be ligated at any time in the 6th instar and still develop into headless pupae and adults. Moreover, when treated with juvenoids the ligated larvae were subjected to the same inhibition of metamorphosis as were normal feeding larvae. It was therefore advantageous to use ligated larvae for O_2 consumption measurements because variations due to differences in locomotory activity and food digestion were thereby avoided.

Figure 3 presents a comparison of O_2 consumption curves of normal last instar larvae and of individuals ligated shortly after ecdysis. In both instances the larvae

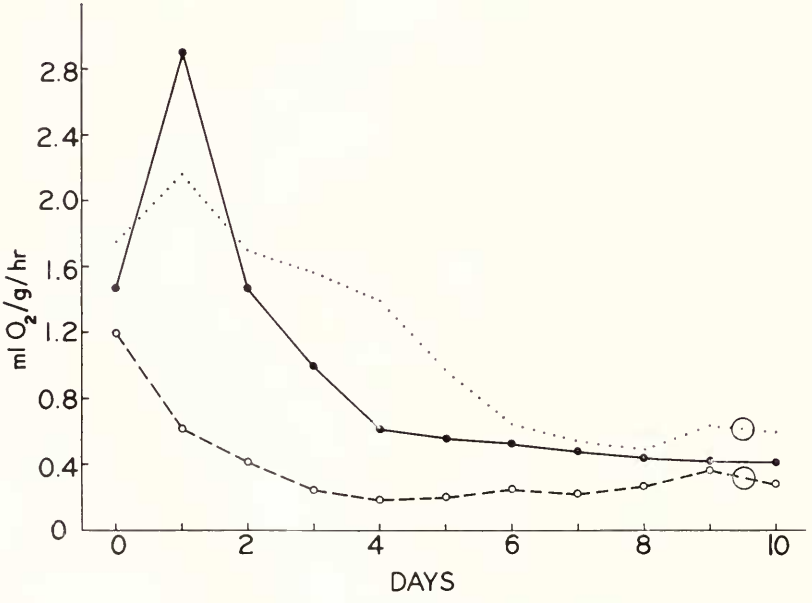

FIGURE 3. O_2 consumption of the last instar larvae which were ligated behind the head just after ecdysis (broken line; n = 5 specimens) or ligated and simultaneously treated with 50/μg/specimen of the juvenoid (full line; n = 6 specimens). The dotted line is taken from Fig. 1 and shows O_2 consumption of normal feeding larvae. Small rings indicate ecdysis or cryptoecdysis, respectively.

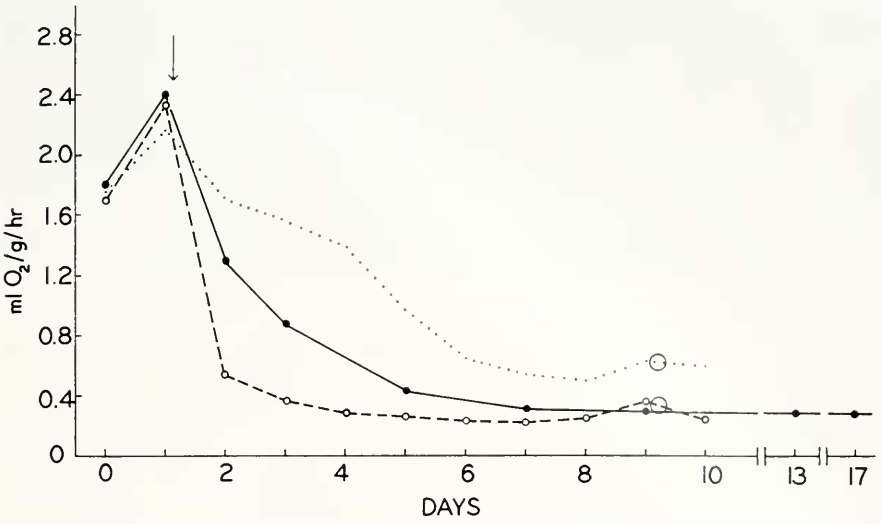

FIGURE 4. The same as in Fig. 3 with exception that the ligatures and juvenoid treatments were made after one day of feeding, as indicated by an arrow (full line; n = 10 specimens; broken line; n = 5 specimens).

developed into pupae after 9 to 10 days. The relatively low rates of O_2 consumption of the ligated larvae show that the processes of larval-pupal transformation alone have considerably smaller energetic requirements than do locomotion and food metabolism. The remaining curve in Figure 3 show the course of O_2 consumption in ligated larvae treated with juvenoid. Except for the first day after treatment their rates of O_2 consumption were less than that of normal feeding larvae. These ligated and treated larvae with completely inhibited metamorphosis maintain a higher metabolic rate than the untreated ligated controls. This suggests that juvenoids may induce certain metabolic changes even in the non-feeding larvae. However, the relative intensity of these metabolic changes is only a small portion of that encountered after hormonal treatment of feeding individuals.

Similar measurements on larvae that were ligated and treated with juvenoid after one day of feeding show basically the same relationships as have been described in the former experiment (*cf.* Figs. 3 and 4). Due to an increased content of reserve materials in the body the larvae which were ligated and treated with juvenoid after one day of feeding had a considerably improved rate of survival. They could be stored for several weeks without developmental changes. These dauerlarvae were used for most experiments with ecdysterone (see below). These results, and other evidence which will be published elsewhere, suggest that most but not all of the hypermetabolism is clearly dependent on the presence of metabolic substrates derived from the ingested food.

Juvenoid effects on metabolism during the pupal-adult transformation

As in most Endopterygote insects, the O_2 consumption rate of *D. vulpinus* followed a typical U-shaped metabolic curve which is characteristic for meta-

morphosis. At the time of pupal ecdysis (day −1 to 0 in Fig. 5) there occurs a temporary small peak in O_2 consumption which is associated with ecdysial functions. Approximately between day 1 and 2 there occurs adult apolysis in the untreated control pupae. This is followed by pharate adult development which culminates by adult ecdysis at day 7. More important for our study are newly found changes in O_2 consumption which reveal the course of metabolic processes during development of two extra pupal instars. This developmental feature was achieved by a single topical treatment of prepupae with large doses (100 μg per specimen) of the juvenoid. The results in Figure 5 show that the extra pupal

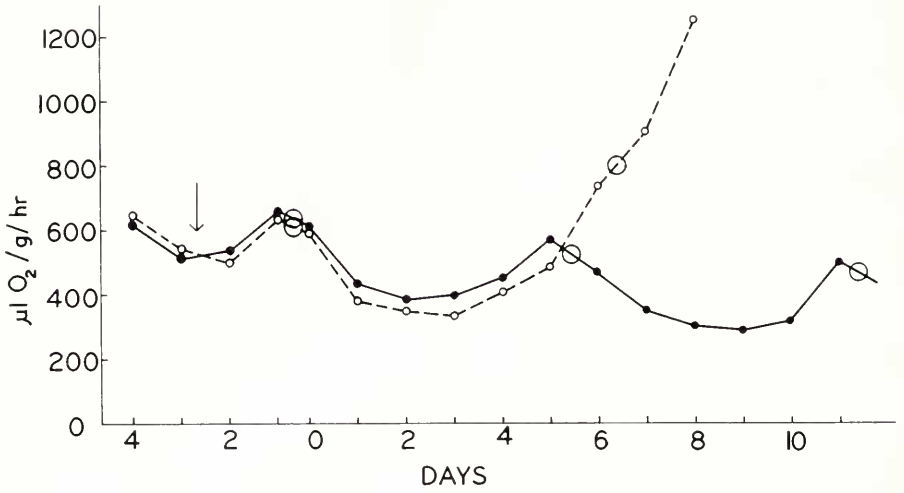

FIGURE 5. Changes in O_2 consumption rate during the prepupal period, in the pupal instar, and at the beginning of adult life in untreated controls (broken line; n = 10 specimens). Small rings on the curve indicate the moments of larval-pupal and pupal-adult ecdyses. Full line (n = 14 specimens) indicates changes in O_2 consumption rate during development of two successive extra-pupal instars induced by a single topical treatment with 100/μg of juvenoid per specimen at the moment indicated by arrow. Small rings on the curve indicate larval-pupal ecdysis, cryptoecdysis of the first extra-pupal instar and cryptoecdysis of the second extra-pupal instar.

molt cycles bring about specific modification of the normal U-shaped metabolic curve. This may be associated with a different type of growth among the tissues. While the untreated group of pupae underwent a pharate adult development from day 1 to day 7, the treated group of pupae underwent development simultaneously without morphogenesis resulting in the formation of first extra pupal instar at day 5 (this stage is usually referred to as second pupa or deuteropupa). Formation of the first extra-pupal instar is then followed by development of the second extra-pupal instar the cuticle of which is fully formed around the day 11.

The first and second supernumerary or extra-pupal instars had perfectly developed pupal epidermal patterns. The extra-pupal cuticles were fully formed one or two days earlier than the adult cuticle in untreated controls. They were well sclerotized and pigmented and the old endocuticle of the previous instars was

regularly digested. However, in spite of the presence of these typical symptoms of ecdysis, the actual act of eclosion from the old exuvia never occurred in any of these stationary pupal-pupal molts.

In individual O_2 consumption curves for each specimen, we have observed that the mentioned modification of the U-shaped metabolic pattern appears also in a few instances where still a third extra-pupal development (not shown in Fig. 5) has taken place. We thus induced a series of several pupal-pupal molts with inhibited morphogenesis which were analogous to larval-larval molts as seen in normal development. However, in contrast to the larval molt cycles the induced repetitions of pupal molts were not connected with somatic growth.

Metabolism during the ecdysterone-induced molt cycles

In the feeding period of the last larval instar, ecdysterone (10 μg/specimen) caused more or less opposite effects to juvenoids. For instance, juvenoids increased the rate of feeding and stimulated hypermetabolism while ecdysterone suppressed or completely abolished feeding and reduced metabolic rate. It is possible that such an inhibitory effect of ecdysterone is partly related to hyperecdysonism (*cf.* Williams, 1968). In contrast to juvenoid applications, all larvae injected with these large doses of ecdysterone underwent precocious molt in 3 days.

The experiments with ecdysterone in the feeding or starved larvae did not allow us to identify an exact proportion of the metabolic intensity which would be attributed to the induced molt cycles. This was caused by relatively large variations in O_2 consumption due to differences in feeding and locomotory activity. Our attention was centered on immobile last instar larvae with inhibited metamorphosis. These were obtained from larvae that had been ligated and simultaneously treated with the juvenoid (50 μg/specimen) after one day of feeding. From the moment of juvenoid application the process of metamorphosis was completely inhibited and the larvae remained for weeks at the morphogenetic stage corresponding to the one-day-old last instar larvae. The initial course of O_2 consumption of these ligated dauerlarvae has been given in Figure 4. Approximately 15-day-old dauerlarvae maintained a very steady rate of O_2 consumption. This allowed one to distingush accurately even small changes in O_2 consumption.

Injections of small amounts of ecdysterone into 15-day-old dauerlarvae restored the larval-pupal molt cycles. Approximately 6 to 7 days after injection there appeared morphologically perfect headless pupae with fully pigmented pupal cuticle (Fig. 6A). After injections the rate of O_2 consumption was increased but this was later followed by a U-shaped curve of O_2 consumption prior to pupation. This metabolic pattern induced by small amounts of ecdysterone (0.5 μg/specimen) is similar to that found before pupation in the normal development (*cf.* Figs. 1 and 6A). The controls injected with solvent did not develop at all. They exhibited an injury effect on O_2 consumption which did not last for more than about 24 hr.

When injected with large doses of ecdysterone (10 μg/specimen), all the dauerlarvae underwent an extra-larval molt in 3 days. The extra larvae showed reduced bristles and incomplete dark larval pigmentation on some parts of the body. It is worthwhile to note that the same effect was also obtained when ecdysterone was directly injected into one-day-old normal last instar larvae. Some of the extra larvae continued to develop into morphologically perfect but headless

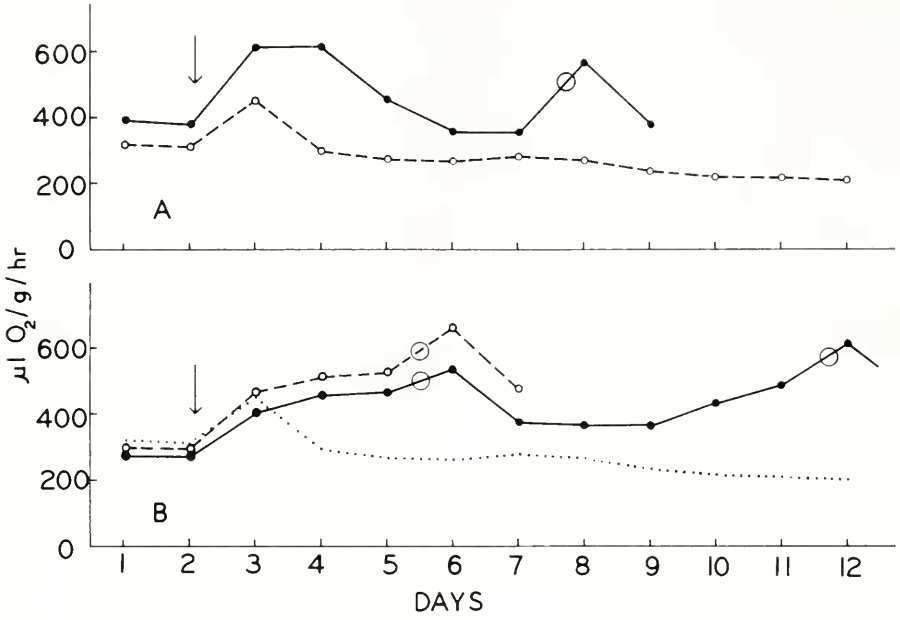

FIGURE 6. Effect of ecdysterone on O_2 consumption of the dauerlarvae. These were obtained by ligaturing behind the head and by topical treatment with 50/µg/specimen of the juvenoid in the one-day-old last instar larvae. The injections of ecdysterone, which are indicated by arrows, were made when the dauerlarvae were 15 to 20 days old. **A** shows the O_2 consumption of specimens injected with 0.5/µg of ecdysterone. These developed into headless pupae after 6–7 days (full line; n = 5 specimens out of 10 individual O_2 consumption curves). Small ring indicates larval-pupal cryptoecdysis. Broken line shows O_2 consumption of the controls injected with equal amounts of the solvent solution (n = specimens). **B** shows the O_2 consumption of specimens which received 10/µg of ecdysterone. Broken line (n = 15 specimens) represents larvae which exhibited extra-larval cryptoecdysis (indicated by small ring) and died afterwards. Full line (n = 5 specimens out of 10 individual curves) represents larvae which exhibited extra-larval cryptoecdysis and then pupal cryptoecdysis which is indicated by second ring. The dotted line is taken from Figure 6A and shows O_2 consumption of the controls.

pupae. As seen in Figure 6B, there was no remarkable difference between the injury response of controls and the ecdysterone injected larvae during the initial 24 hr period. Later, at the 2nd and 3rd day when the injury metabolism has faded out, the dauerlarvae injected with ecdysterone respired at about twice the rate of the controls. And there appeared also a small peak in O_2 consumption indicating unsuccessful ecdysis. Specimens which developed further into pupae after having experienced the extra-larval molt exhibited a similar type of the U-shaped metabolic course as in Figures 1, 3 and 6B.

It may be anticipated that differences in O_2 consumption between the controls with completely inhibited morphogenesis and the ecdysterone injected specimens undergoing extra-larval or larval-pupal molts would indicate approximately the amount of metabolic energy required for performance of the respective molt cycles. Our results have demonstrated that in relation to certain physiological functions such as are food digestion and intensive locomotion, the energetic requirements for

the morphogenetic process alone are relatively minor. This conclusion is supported by the drastic changes in respiratory metabolism which take place during the 3-day larval-larval molt cycle in the growing 5th instar larvae (*cf.* Fig. 1) in contrast to a relatively small increase in metabolic intensity found in the ecdysterone induced 3-day larval-larval molt cycles which take place in the non-feeding ligated dauer-larvae (Fig. 6B).

Because our measurements were performed in daily intervals they would not record any possible short-term effects of ecdysterone on O_2 consumption. For this reason we performed an additional experiment with the injections of large doses of ecdysterone into the above described dauerlarvae. The O_2 consumption rate was then measured in successive one hr intervals during 24 hrs. The results are shown in Figure 7. It appears that the ecdysterone treated specimens have a slightly

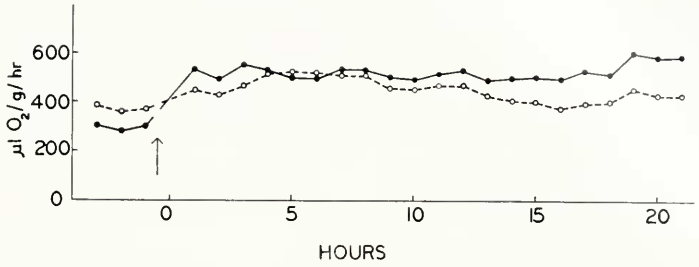

FIGURE 7. Same as in Figure 6B except that O_2 consumption readings were taken in 60 min intervals (full line; n = 8 specimens). Broken line (n = 5 specimens) shows O_2 consumption of the controls injected with the solvent alone. The arrow indicates the moment of injection.

elevated respiratory rate during the initial 5 hr period after the injection. We are not certain, however, whether this is a specific response to ecdysterone or merely a result of variability in responses to epidermal injury. Somewhat later, from 7 hr after injections, the individual variations in O_2 consumption diminished. Subsequently, the ecdysterone treated specimens exhibited slow but continuous increase in O_2 consumption rate over the control level.

DISCUSSION

Several authors studying the effect of hormones on respiratory metabolism in insects came to the conclusion that the effects were indirect depending on the degree of morphological and physiological changes induced in the reacting tissues (Pflugfelder, 1952; Neugebauer, 1961; Novák and Sláma, 1964, 1965, 1968, 1971; Lüscher and Leuthold, 1965; Wigglesworth, 1965b; Sehnal and Sláma, 1966). Our results with the bioanalogues of insect hormones are in full accord with this conclusion. We have demonstrated that juvenoids can cause enormous increases of respiratory metabolism when applied at certain periods in insect development whereas they are ineffective or cause completely different metabolic responses when applied at some other developmental period. Similarly, ecdysterone has a depressive metabolic influence when injected into feeding larvae although it stimulates metabolism in connection with induced molt cycles.

The results obtained in *D. vulpinus* also support earlier assumptions (Sláma, 1968, 1971; Sehnal and Sláma, 1966; Sláma *et al.*, 1974) that each of the hormonally conditioned developmental cycles in insects is characterized by certain specific patterns of total body metabolism. A retrospective look into literature on metabolism during insect postembryonic development (Kuznetzov, 1953; Wigglesworth, 1965a) reveals that the basic type of metabolic changes described here for the larval-larval, larval-pupal, and pupal-adult molt cycles may be a rather common phenomenon among insects belonging to quite different taxonomic groups. It is obvious from the results that the quality and timing of action of the hormones are essential for determination of the respective category of the developmental and metabolic cycles. However, the present findings on *Dermestes* also indicate that the metabolic responses of the tissues are not solely dependent on the hormonal milieu but are also subject to different feed-back reactions which may be mediated by nutritional conditions, availability of endogenous metabolic substrates, ontogenetic stage of the cells, *etc.*

The modified U-shaped metabolic pattern found in the experimentally induced extra-pupal instars of *Dermestes* appears to be very similar to that observed by Gilbert and Schneiderman (1961) and Steen (1961) in saturniid pupae treated with Cecropia extracts containing juvenile hormone. In addition, similar modification of the U-shaped metabolic curve in metamosphosis of *Tenebrio* has been found by Schmialek and Drews (1965) and by Geyer, Herda and Schmialek (1968) after treatments with farnesol derivatives. In all these instances the main difference between the juvenile hormone induced extra-pupal development and the normal adult development was the absence of elevated respiration which normally occurred prior to adult eclosion. This metabolic increase is associated among other factors with an extensive development of imaginal thoracic musculature. Because growth and differentiation of adult thoracic muscles are inhibited during the extra-pupal development, we assume that the absence of adult musculature may well account for the mentioned differences in metabolism.

The most spectacular effect of hormone analogues in *Dermestes* is undoubtedly the hypermetabolism in the final larval instar. In normal development, the young larval-larval instars which are commonly believed to develop in the presence of a high titre of juvenile hormone, have as a rule much higher respiratory metabolism (per unit of live weight) than the last instar larvae. In *Galleria* for example, the extra-larval molt cycles induced by implantations of *corpora allata* also show increased rate of respiratory metabolism. In addition, the extra-larval development has shown a type of metabolic course similar to that normally found in the penultimate and younger larval instars (Sehnal and Sláma, 1966). In *Galleria*, however, the metabolic increase associated with the extra-larval development was relatively small compared with hypermetabolism in *Dermestes*, where the tremendous metabolic stimulation was not a result of an extra-larval molt cycle.

The values of respiratory quotients, which are close to 0.7 during hypermetabolism, suggest that oxygen-poor substrates such as are lipids are being metabolized. Provided that this can be confirmed by a direct lipid analysis it would then indicate that hypermetabolism in *Dermestes* may represent a reciprocal effect to allatectomy which is commonly associated with decreased lipid metabolism and their accumulation in the body (Engelmann, 1970).

Since most of the compounds with juvenile hormone activity are oxygen-poor isoprenoids rich in methylene groupings, it is also possible that these compounds will be increasingly metabolized during hypermetabolism. This idea is supported by our observations that feeding larvae which show hypermetabolic responses require up to 100 times larger doses of juvenoid for the 5-day delay in pupation than do ligated larvae where hypermetabolism does not occur. It seems that the body reacts at this critical period at the onset of metamorphosis to the unwanted presence of juvenile activity by mobilizing certain metabolic systems for its deactivation or excretion. We are convinced that the hypermetabolism constitutes a part of the physiological "anti-juvenile" mechanisms which are known to operate in the last larval instar of this species (Sláma *et al.*, 1974).

It has been reported recently (Whitmore, Gilbert and Ittycheriah, 1974) that juvenile hormone applied to saturniid pupae induces formation of carboxyesterase enzymes which in turn inactivate the juvenile hormone esters. At present we have no evidence to show that an increased ester hydrolysis (which also involves splitting of glycerides) would be associated with hypermetabolic responses to juvenoids in *Dermestes*.

In contrast to the extensive amount of data on various biochemical effects of ecdysoids, our knowledge concerning their effects on total body metabolism is mainly based on indirect evidence derived from metabolic changes in metamorphosis and postdiapause development. The results obtained with ecdysterone in *Dermestes* suggest that the mode of action of this hormone does not depend on an immediate metabolism stimulating effect. Its depressive effects on metabolism of feeding larvae can be explained by precocious secretion of the new cuticle during which process the larvae usually stop feeding and reduce locomotion. On the other hand, in the non-developing and immobile stages, with low basal metabolism of maintenance, ecdysterone clearly stimulates more or less pronounced elevation of the metabolic rate. Changes in metabolism that follow later after ecdysterone injections are determined by the type and extent of the morphogenetic events, *i.e.*, by the respective category of the developmental cycle in question.

Summary

1. Treatment of the early last instar larvae with juvenoids caused enormous increase in respiratory metabolism which is referred to as hypermetabolism. During this process the larvae consumed as much as 10 ml of oxygen per gram live weight per hour. It is anticipated that hypermetabolism constitutes part of a physiological "anti-juvenile" mechanism in *Dermestes*. The effect is associated with considerably enhanced food consumption and excretion. The phenomenon was virtually absent when juvenoids were applied to non-feeding larvae or pupae.

2. Single treatment of prepupal stages with large doses of juvenoids induced the formation of several extra-pupal instars. Each of them exhibited a slightly modified type of the U-shaped metabolic course.

3. Ecdysterone caused an indirect inhibition of the total body metabolism in the feeding larvae. In the non-feeding, immobile dauerlarvae it slowly increased the metabolic rate over the low maintenance level. In connection with stimulation of the molt cycles by ecdysterone there were specific patterns in respiratory metabolism which corresponded to the larval-larval or larval-pupal development.

4. Both the hormonal bioanalogues, *i.e.*, juvenoids and ecdysterone, are believed to have an indirect effect on the total body metabolism. The effect depends on the quality and degree of morphological and physiological changes conditioned by the hormonal milieu and on certain feed-back reactions. It has been confirmed that each of the developmental cycles in insects, such as are larval-larval, larval-pupal, and pupal-adult molt cycles, can be also characterized by a specific pattern in the course of respiratory metabolism.

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